Crop Protection 28 (2009) 1007–1011

Contents lists available at ScienceDirect

Crop Protection

journal homepage: www.elsevier.com/locate/cropro

Short communication

Sweet potato leaf curl virus: Efficiency of acquisition, retention and transmission by *Bemisia tabaci* (Hemiptera: Aleyrodidae)

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ARTICLE INFO

Article history:
Received 3 February 2009
Received in revised form
22 June 2009
Accepted 26 June 2009

Keywords:
Begomovirus
Ipomoea
Bemisia tabaci
B-biotype sweetpotato whitefly
SPLCV
Virus

ABSTRACT

The sweetpotato whitefly, *Bemisia tabaci* (Gennadius), vectors numerous plant viruses, including *Sweet potato leaf curl virus* (SPLCV), a begomovirus. Experiments were conducted on seedlings of an indicator plant, the Brazilian morningglory (*Ipomoea setosa* Ker Gawl.), and sweet potato [*Ipomoea batatas* (L.) Lam.] to assess acquisition, retention and transmission of SPLCV by *B. tabaci*. Assays were based on the ability of the adult whitefly to acquire and transmit the virus. Two independent techniques, based on the expression of symptoms on the indicator plants and the detection of SPLCV with real-time polymerase chain reaction, were used to indicate SPLCV infection. The acquisition time of SPLCV by adult *B. tabaci* was 24 h and reached 100% by 84 h of exposure. Retention of SPLCV infectivity by viruliferous adults reached up to 30 days on non-SPLCV host plants (collard, *Brassica oleracea* ssp. *acephala* de Condolle). In transmission tests, a minimum of 15 min was required for a viruliferous whitefly population to transmit the virus to *I. setosa*. The efficiency of transmission increased over time; however, only 60% of the assay plants were infected after exposure to viruliferous whiteflies for 48 h. Male and female adult whiteflies vectored SPLCV with similar efficiency. Findings from this study will help to understand the epidemiology of SPLCV in sweet potato fields, and ultimately in the management of this disease. Such detailed investigations to assess vector behaviors also have implications in the study of other whitefly-virus systems among agricultural crops.

1. Introduction

The B-biotype sweetpotato whitefly [*Bemisia tabaci* (Gennadius)] and other members of the *Bemisia* complex are serious global pests of agricultural crops, including sweet potato [*Ipomoea batatas* (L.) Lam]. *B. tabaci* is a highly adaptive pest which feeds on diverse plant species (Greathead, 1986; Oliveira et al., 2001) and new hosts continue to be identified (Simmons et al., 2008). It vectors over 100 plant viruses (Jones, 2003). The wide polyphagous habit of *B. tabaci* increases the probability of it to acquire and disseminate plant viruses from weeds or other plants.

Brazilian morningglory, *Ipomoea setosa* Ker Gawl., exhibits prominent visible symptoms to several sweet potato viruses. Thus, *I. setosa* is commonly used to detect viruses in sweet potato cultures through grafting (Moyer et al., 1989). In recent years, polymerase chain reaction (PCR) has been demonstrated to be an effective method of detecting these viruses (Lotrakul et al., 2002; Li et al., 2004). Subsequently, real-time PCR was demonstrated to be a more efficient method in detecting begomoviruses in sweet potato than conventional PCR (Kokkinos and Clark, 2006). *Sweet potato leaf curl virus* (SPLCV) was first reported in Taiwan and Japan (Chung et al., 1985; Osaki and Inouye, 1991). Subsequently, this virus has been detected in the United States (Lotrakul et al., 1998), Spain [where it was initially reported as *Ipomoea yellow vein virus* in *Ipomoea indica* (Burm.) Merr.] (Banks et al., 1999), Peru (Fuentes and Salazar, 2003), Italy (Briddon et al., 2006), Kenya (Miano et al., 2006), China (Luan et al., 2006), India (Makeshkumar et al., 2007) and Republic of Korea (Kwak et al., 2007). SPLCV is transmitted by *B. tabaci*, but not by the bandedwinged whitefly, *Trialeurodes abutilonea* (Haldeman) (Valverde et al., 2004). However, information on the efficiency of SPLCV acquisition, retention and transmission by *B. tabaci* was limited (Valverde et al., 2004).

Understanding the interaction of insect–plant–virus relationships is essential epidemiological knowledge for effective crop management. Sweet potato is a vegetatively propagated crop; its root stocks and cuttings are potential carriers of the virus. However, disease epidemiology depends on the efficiency of the vectoring whitefly population in acquisition, retention and transmission of SPLCV. Because symptoms expressed on the SPLCV-infected sweet potato can be mild or non-existent, a sensitive indicator plant (e.g., *I. setosa*) along with real-time PCR may be used to determine virus

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0261-2194/$ – see front matter © 2009 Published by Elsevier Ltd.
doi:10.1016/j.cropro.2009.06.011

infectivity on assay plants. We conducted experiments to assess acquisition, retention, and transmission of SPLCV by *B. tabaci*.

2. Materials and methods

2.1. Source of whiteflies and virus

A SPLCV culture was established through transmission using adult whiteflies (*B. tabaci*) feeding on sweet potato from a research greenhouse in Charleston, SC in 2006. SPLCV-infected vine cuttings in vials of water were placed in a cage with adult B-biotype *B. tabaci* and held in the laboratory. The whiteflies were from a greenhouse colony that had been maintained on a non-SPLCV host plant, collards (*Brassica oleracea* ssp. *acephala* de Condolle), before being used for virus acquisition. After one week of feeding on SPLCV-infected sweet potato cuttings, the viruliferous adult whiteflies were aspirated and released onto three *I. setosa* seedlings (three leaf stage) in three separate cages. Each cage consisted of a clear plastic cylinder container (18 cm tall by 20 cm diameter) in which fine mesh screening was secured across the top with rubber bands. About 50 viruliferous whiteflies were released into each cage. Three additional *I. setosa* seedlings were similarly caged and held without whiteflies as a control. Three weeks after their exposure to the whiteflies at $26 \pm 0.5\ ^{\circ}C$, all three assay *I. setosa* plants began to exhibit mosaic symptoms. Presence and identity of SPLCV was verified using real-time PCR. All control plants were healthy looking and tested negative for SPLCV by real-time PCR. These SPLCV-infected *I. setosa* plants were used to establish a colony of viruliferous whiteflies in the laboratory. Also, a clean (SPLCV-free) whitefly laboratory colony was established on non-SPLCV host collard plants.

2.2. Isolation of total plant DNA and real-time PCR detection of SPLCV

We adapted the real-time PCR that was developed by Kokkinos and Clark (2006) to supplement the symptom expression as observed on the tested *I. setosa* or sweet potato plants. Total plant DNA extraction was carried out with leaf tissue collected from each test plant using a Qiagen DNeasy plant kit (Qiagen, Valencia, CA). Leaf tissues from healthy *I. setosa* seedlings as well as SPLCV-infected plants were used for negative and positive controls, respectively.

2.3. Viral acquisition assay

To assess the efficiency of *B. tabaci* in acquiring SPLCV, a time course study was conducted. Three SPLCV-infected *I. setosa* plants were placed in a $61 \times 61 \times 61$ cm BugDorm-2® (BioQuip Products, Rancho Dominguez, CA) insect cage. All adults, large nymphs and pupae of *B. tabaci* were removed from the plants so that only insects from the virus-free colony would be used in this test. Then, ≈ 1200 virus-free adult whiteflies were aspirated into vials and released onto the caged source SPLCV-infected plants. Insects were released below the apical expanded leaves so that most landed on the bottom surface of leaves immediately after release. At each exposure time interval, 3 sets of 10 adult whiteflies were aspirated from leaves of infected plants into separate vials and each set of whiteflies was immediately released into a separate cage containing a first-leaf stage indicator *I. setosa* seedling. Three plants were tested at each time intervals of 0, 0.25, 0.5, 1, 2, 4, 6, 12, 24, 36, and 48 h. A zero time interval consisted of plants with whiteflies from the virus-free colony. After samples were taken at the end of each time interval, except for the zero and the last interval, all whiteflies that were on the walls of the cage were removed and discarded. Tested plants in cages were held in an environmental chamber maintained at $26 \pm 0.5\ ^{\circ}C$, 75–85% RH, and 16:8 h light:dark regime and watered through the screening as needed. After 30–60 days, the plants were observed for mosaic and/or leaf curl symptoms, and the presence of SPLCV was confirmed by real-time PCR using DNA samples prepared on the tested plants. In a second experiment, time intervals were extended to include 60, 72 and 84 h in acquisition access periods.

2.4. Viral retention assay

In a retention assay, trials were conducted to determine how long SPCLV infectivity in the viruliferous adult whitefly population could be maintained after being transferred to non-SPLCV host plants. To achieve a complete viruliferous whitefly population, 3000 adult *B. tabaci* were aspirated into a BugDome-2® cage housing SPLCV-infected *I. setosa* plants for 3 days of acquisition access period as determined above. This viruliferous adult whitefly population was then transferred by aspiration and maintained on a tray of collard (a non-SPLCV host) seedlings in another BugDome-2® cage. To avoid any new adult whiteflies from deposited eggs, the collard seedlings were replaced every 10–14 days. On the start day and on each 5-day interval, 3 samples of 10 unsexed adult whiteflies were collected from the collards. Each sample was released into a cylindrical cage containing a cotyledon stage *I. setosa* seedling. Assay plants were maintained in an environmental chamber as described above for 30–60 days. Viral infection of the recipient *I. setosa* plants was examined based on the expression of symptoms, and the presence of SPLCV was confirmed by real-time PCR. The experiment was repeated using 4000 adult whiteflies.

2.5. Viral transmission assay

Initial transmission assays were conducted using *I. setosa* indicator plants with adult *B. tabaci*. Viruliferous whiteflies from the SPLCV-infected colony were allowed feeding access on clean recipient *I. setosa* plants for 0–48 h. Cotyledon stage *I. setosa* indicator plants were set up in above-described cylindrical cages. In each cage for time series in excess of 1 h, 10 adult viruliferous whiteflies were released to each *I. setosa* plant. At the end of each transmission time series (± 5 min), all whiteflies were aspirated from the seedling. Each test plant was then placed in a clean cylinder cage, covered with screening, and returned to the environmental chamber as described above for 21–30 days. For time series of 1 h or less, each test plant was held in a BugDome-2® cage, at $26\ ^{\circ}C$ and continuous light condition. For these time series, 10 adults were released below the cotyledons, and were aspirated from the plant after exposure periods of 0.25, 0.5 or 1.0 h (± 1 min). Each plant was then placed in a cylindrical cage and maintained as described above. The assay plants were evaluated for viral symptoms, and the presence of SPLCV was confirmed through real-time PCR. Three plants were assayed per exposure time. The experiment was repeated four times. However, appropriate exposure time was adjusted following results of the initial trial.

To investigate whether the transmission efficiency observed on *I. setosa* was applicable to sweet potato, additional transmission trials were carried out on sweet potato seedlings. Cotyledon stage sweet potato seedlings were used as recipient plants. We established the seedlings from sweet potato seeds to ensure the testing materials were free of any sweet potato viruses. No known sweet potato virus has been shown to be seed-borne. Assay plants were sampled 30–60 days after exposure to whitefly feeding. Leaf curl and mosaic symptom expressions were noted and confirmation of the presence of SPCLV was carried out by real-time PCR. The experiment was repeated three times.

2.6. Efficiency of whitefly gender on viral transmission

A test was conducted to compare the efficiency of transmission of SPLCV by adult male and female *B. tabaci*. A single adult male whitefly was aspirated from SPLCV-infected *I. setosa*, and released into a cylindrical cage (described above) containing a healthy recipient cotyledon stage *I. setosa* plant. The cage was covered with screening and held in an environmental chamber as described above. The same setup was done for each single adult female whitefly. A total of 14 adults of each sex were set up in this manner. Additional plants were each set up with a non-infected male whitefly, a non-infected female whitefly, and no-whitefly as checks. After 30 days, test plants were evaluated for symptom expression and confirmation of the presence of SPLCV using real-time PCR. The experiment was repeated three times. Incidence of transmission by sex was compared using the t-test procedure in SAS (SAS Institute, 2002).

3. Results

3.1. Acquisition

The minimum acquisition access period required for adult whiteflies to acquire SPLCV and effectively vector the virus to the assay plants was 24 h. There was no SPLCV infection on assay plants observed in repeated tests in 12 h or less of the acquisition access period (Table 1). However, 16% or more of the plants became infected with SPLCV from whiteflies when acquisition time periods were increased to $\geq$24 h (Table 1). By 84 h, all assay indicator plants became infected with SPLCV based on both DNA analyses and expression of viral symptoms.

3.2. Viral retention

Viruliferous adult *B. tabaci* retained and transmitted SPLCV for up to 30 days after being removed from the SPLCV inoculum source (Table 2). Not all recipient plants were infected with SPLCV (only 83.3% infection) on the starting date (Table 2). A high transmission rate (83.3%) was maintained by the whiteflies for at least 5 days. Thereafter, there was a decline in the incidence of transmission. By day 30, transmission was reduced to 16.7%. Transmission was lost by day 35, and no transmission was detected through day 50. By the last sample date of each trial, only a few (<100) adult whiteflies remained alive.

Table 1
Time for acquisition of *Sweet potato leaf curl virus* (SPLCV) by B-biotype *Bemisia tabaci* based on its transmission to and viral DNA detection from indicator plants (*Ipomoea setosa*) maintained at 26 °C.

Time (h) after exposure to infected plants	Number of plants tested	Number of indicator plants infected with SPLCV (%)
0.0	6	0 (0)
0.25	6	0 (0)
0.5	6	0 (0)
1.0	6	0 (0)
2.0	6	0 (0)
4.0	6	0 (0)
6.0	6	0 (0)
12.0	6	0 (0)
24.0	6	1 (16.7)
36.0	3	1 (33.3)
48.0	6	2 (33.3)
60.0	3	1 (33.3)
72.0	3	2 (66.7)
84.0	3	3 (100)

Table 2
Duration of retention of *Sweet potato leaf curl virus* (SPLCV) by B-biotype *Bemisia tabaci* based on its transmission to and detection of viral DNA from indicator plants (*Ipomoea setosa*) maintained at 26 °C.

Time (day) after exposure to infected plants	Number of plants tested	Number of indicator plants infected with SPLCV (%)
0	6	5 (83.3)
5	6	5 (83.3)
10	6	2 (33.3)
15	6	1 (16.7)
20	6	2 (33.3)
25	6	0 (0)
30	6	1 (16.7)
35	6	0 (0)
40	6	0 (0)
45	3	0 (0)
50	3	0 (0)

3.3. Transmission

SPLCV was detected in *I. setosa* with only 15 min of exposure to viruliferous whiteflies, and the incidence of viral infection increased over time (Table 3). Transmission reached 62.5% by 48 h, although there were fluctuations in the data across the exposure periods (Table 3). In using sweet potato as indicator plants, SPLCV was not detected in sweet potato with exposure periods of less than 6 h; 37.5% of the plants were infected by 48 h (Table 3). Data with sweet potato, suggest that there may be a host affect (as compared with *I. setosa*) on infection (Table 3). The cotyledon of sweet potato (4.2 cm^2) was much smaller ($P < 0.001$) than that of *I. setosa* (18.4 cm^2), and behavior for attraction, settling or feeding may have differed between the groups of whiteflies on the two plant species. Nevertheless, SPLCV was efficiently transmitted to sweet potato by adult whiteflies.

3.4. Efficiency of whitefly gender on viral transmission

Investigation into a possible efficiency disparity of SPLCV-transmission between males and females, revealed that both sexes of *B. tabaci* acquired SPLCV from infected *I. setosa* plants and transmitted the virus to uninfected *I. setosa* plants. Body size might be related to transmission of SPLCV due to the quantity of viral particles that the larger females may acquire as compared with smaller males. However, even with a trend of higher incidence of transmission by the female, there was no significant difference ($P > 0.13$, $DF = 82$, $t = 1.51$) in transmission between the sexes. Only $4.8 \pm 3.2\%$ of the males and $10.7 \pm 3.6\%$ of the females were successful in infecting the recipient plants. All control plants remained healthy and were negative for SPLCV.

Table 3
Time for transmission of *Sweet potato leaf curl virus* (SPLCV) by B-biotype *Bemisia tabaci* based on its transmission to and detection of viral DNA from plants maintained at 26 °C.

Time (h) after exposure to infected plants	*I. setosa* plants infected with SPLCV		*I. batatas* plants infected with SPLCV	
	No. of samples	%	No. of samples	%
0.0	12	0	3	0
0.25	10	20.0	3	0
0.5	12	16.7	6	0
1.0	9	0	6	0
2.0	9	11.1	3	0
4.0	6	0	3	0
6.0	12	41.7	8	12.5
12.0	12	25.0	6	16.7
24.0	12	25.0	9	0
36	6	33.3	6	0
48	16	62.5	8	37.5

4. Discussion

Results support that with the availability of virus inoculum and the relatively efficient transmission of SPLCV by whiteflies, SPLCV could potentially have devastating effects on sweet potato production. With further movement of *B. tabaci* and ever increasing host range (Simmons et al., 2008), it is anticipated that SPLCV will have a greater impact on the sweet potato industry in the United States and other parts of world. Because sweet potato is vegetatively propagated, viral infections are passed on and accumulated over years. Thus, planting virus-tested and certified sweet potato will reduce the chance for the whitefly to acquire SPLCV. We determined that it took 12 h or more for successful acquisition of SPLCV to occur. Applications of insecticides may be needed to help manage whitefly populations before they become viruliferous for SPLCV-transmission. The long retention period (30 days) after virus acquisition suggests a single viruliferous whitefly can have ample time to cause serious damage after feeding on a SPLCV inoculum source. With its active flying pattern, its natural attraction to sweet potato plants and relatively efficient transmission, the consequence of such a combination could have a serious effect on sweet potato production. Our recent field trial data indicate a 50% yield improvement in SPLCV-free plants generated from meristem shoot-tip culture over that of the SPLCV-infected plants from the same sweet potato cultivars (unpublished). Thus, the findings obtained from this study will help in the understanding of the factors influencing the epidemiology of this relatively new virus on sweet potato and, hopefully, on finding solutions to manage this disease.

In considering vector efficiency, in addition to the duration of exposure time, population density of the vector is important. We used low numbers of insects (1 or 10) in our efficiency experiments. In a related study with SPLCV, Lotrakul et al. (1998) demonstrated an increase in infection with a higher number of whiteflies. In their study on *I. nil* (L.) Roth, a host that is seed propagated, infection increased from about 3 to 50% as the number of adult whiteflies increased from 1 to 40 per plant during a 2-day exposure period. In other research on *I. nil*, transmission of SPLCV was 2–8% for a 2-h exposure when individual adult *B. tabaci* were used (Valverde et al., 2004). Using similar methods, the transmission of a *Crinivirus*, *Sweet potato chlorotic stunt virus*, by *B. tabaci* was only 15% (Sim et al., 2000). Data from our study support a relatively low incidence of infection by a single whitefly. Our findings further suggest that females may be more efficient than males in vectoring SPLCV. In the retention study, insects surviving during the last half of the experiment may have been the youngest of the cohort.

Data from our experiments suggest that *B. tabaci* is less efficient in acquiring SPLCV and in transmitting the virus in sweet potato as compared with other host-virus systems. For example, Jiu et al. (2006) reported that 100% of the insects were infected with two begomoviruses (*Tobacco curly shoot virus* and *Tomato leaf curl virus China*) after 12 h of exposure to 10 *B. tabaci* that fed on infected plants. They found that after 0.5 h, infection of *B. tabaci* was 40% for each virus. In a related transmission study with *Tomato yellow leaf curl China virus*, *B. tabaci* transmitted the virus to 55% of tomato plants by one adult whitefly and 100% of the tomato plants by 10 whiteflies over a 48 h exposure period (Jiu et al., 2006). However, in the same experiment, transmission of *Tobacco curly shoot virus* to tomato was only 0 and 10% by 1 and 10 *B. tabaci*, respectively. Apparently, the efficiency of whitefly transmission depends on virus–host interaction and is also likely affected by environmental conditions.

A combination of biological indication in symptom expression and molecular detection in determining virus identity improve the reliability of viral transmission data. Whitefly populations are naturally of mixed ages in the field, but it is not known if age may affect the vector–virus association. Sweet potato can harbor viruses without displaying symptoms (Moyer et al., 1989). Hence, if a plant does not display virus symptoms, one might conclude that it is negative for the virus. Likewise, molecular detection may pose some degree of uncertainty with possible false negatives and false positives samples for the virus, especially when the virus titer is low. However, when both techniques are used together, reliability of the results is enhanced.

Our study addressed the ability of *B. tabaci* to acquire, retain and transmit SPLCV in *I. setosa* and sweet potato plants. The study herein tested the ability of *B. tabaci* to transmit regardless of any threshold of virus titer in its body. Although each *B. tabaci* was not found to be highly efficient in transmitting this virus, the likelihood of transmission is elevated with increased whitefly numbers and with long exposure times, as are common in fields and production beds. These results will help to understand the epidemiology of SPLCV.

Acknowledgements

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